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Dogs on the catwalk: Modelling re-introduction and translocation of endangered wild dogs in South Africa

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ABSTRACT

In South Africa, a plan was launched to manage separate sub-populations of endangered African wild dogs (*Lycaon pictus*) in several small, geographically isolated conservation areas as a single meta-population. This intensive management approach involves the re-introduction of wild dogs into suitable conservation areas and periodic translocations among them. Despite the initial failures and high costs associated with wild dog re-introductions and translocations, there is no predictive framework available to quantify which management protocol is the most efficient. We therefore developed an individual-based model of wild dog population and pack dynamics, which accounts for the wild dogs' social complexity. The model appeared to capture the essential characteristics of a real wild dog population from Hluhluwe-iMfolozi Park, South Africa and to be relatively robust to parameter uncertainty, suggesting that the model is valid enough for addressing management problems. The model enabled us to quantify a critical initial number of packs (two) and individuals per pack (six) necessary for a re-introduced wild dog population to establish itself in the release area. We also found a practically feasible intervention regime at which a re-introduced wild dog population had the best chance of persistence: intermittently adding packs (at least every 6 years) and harvesting disperser groups (as often as every 4 years) for translocation to other release sites, without threatening the small source population. This study demonstrates that individual-based models can be a powerful decision-support tool in re-introduction planning and provides insight into how populations made up of social groups have dynamics, and ultimately persistence, determined by individual behaviour.

1. Introduction

Population viability analyses aim at making relative predictions regarding which management measures will be most effective in enhancing population persistence (Possingham et al., 2001). Simple models may be best for population viability analyses because more detailed and complex models can be too uncertain due to error propagation (Morris and Doak, 2002). However, classical population models and generic software packages cannot capture the critical effects of behavioural features, such as group living, on population persistence. Some individuals in a group may be less affected by, and thus buffered from, environmental variation (Grimm et al., 2005a), and such effects are important for modelling the dynamics of many group living species (e.g. Vucetich et al., 1997; Grimm et al., 2003). Individual-based models enable us to explore how population characteristics emerge from the ways in which individuals interact with each other (DeAngelis and Gross, 1992; Uchmański and Grimm, 1996; Grimm and Railsback, 2005). Individual-based models can be a powerful tool for addressing management problems and prioritizing needs for the conservation of endangered species (Bart, 1995; Lacy, 2000; Petersen et al., 2008).

One intensely social species with a nearly obligate cooperative breeding system that is on the brink of extinction is the African wild dog (*Lycaon pictus*), with fewer than 6000 animals remaining in sub-Saharan Africa (Woodroffe et al., 2004). Most wild dog conservation efforts have focused on the few remaining viable populations in large protected areas. Considering increasingly fragmented landscapes, Mills et al. (1998) proposed a complimentary approach, whereby separate sup-populations of wild dogs in several small, geographically isolated conservation areas in South Africa are managed as a single meta-population. This intensive management approach, to supplement the single viable population occurring in Kruger National Park, involves the re-introduction of wild

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dogs into suitable conservation areas, and periodic translocations among them to mimic natural dispersal and maintain gene flow (reviewed by Davies-Mostert et al., 2009). This conservation strategy is largely based upon expert opinion (Wild Dog Advisory Group of South Africa) and there is no predictive framework available to quantify which management protocol is the most efficient. This is despite the initial failures and high costs associated with wild dog re-introductions and translocations (Lindsey et al., 2005).

Simulation models can, in principle, support the conservation management of wild dogs and a number of population viability analyses have been developed for this species (Burrows et al., 1994; Ginsberg et al., 1995; Ginsberg and Woodroffe, 1997; Mills et al., 1998; Vucetich and Creel, 1999; Cross and Beissinger, 2001; Creel and Creel, 2002; Creel et al., 2004; Vial et al., 2006). However, except for Vucetich and Creel (1999) and to a lesser extent Vial et al. (2006), all existing models ignore the wild dogs' social complexity, which limits the suitability of these models for wild dog population viability analyses. Most notably, the model used for the Population and Habitat Viability Assessment, on which the South African wild dog meta-population management plan is based (Mills et al., 1998), was developed with a generic software package (VORTEX) that is not designed to take into account complex behavioural traits. The model of Vucetich and Creel (1999) includes social interactions, but is focused on interspecific competition with lions (*Panthera leo*), which may not be the critical threat it was once considered (Hayward and Kerley, 2008; Rasmussen et al., 2008). Indeed, our extensive field study on a small re-introduced population of wild dogs, spanning over 25 years, indicates that competition with lions is less important in our study area (see below) and that the process of pack formation is decisive for the success of wild dog re-introductions (Gusset et al., 2006a, 2008a; Somers et al., 2008). There is thus need for a new decision-support tool for re-introduction planning, focusing on behavioural rather than environmental factors.

The success of any re-introduction attempt depends on two factors, namely the re-introduced population reaching the established phase and, once this stage is reached, maintaining itself in the release area (see Grimm and Wissel, 2004 on the importance of this distinction for population viability analyses). For cooperative breeding species like wild dogs, this suggests that the initial number of groups and individuals per group are likely to determine establishment success, whereas persistence is likely to depend on the formation of new groups to maintain the population's reproductive capacity (Courchamp et al., 2000; Courchamp and Macdonald, 2001). This holds until prey requirements are exceeded (Hayward et al., 2007). In wild dogs, new packs typically form when two unrelated opposite sex disperser groups meet and bond (Creel and Creel, 2002). Theoretical models predict that this process could be limited by problems in finding suitable mates when population size is small (Courchamp et al., 2000), and we indeed found such a mate-finding Allee effect at low pack numbers in the wild dog population modelled here (Somers et al., 2008). The observed pattern in pack formation arising from the individuals' interactions thus presents itself as a starting point for designing the model's structure, resolution and processes.

Matrix population models (Caswell, 2001), which can be a powerful tool for projecting the dynamics of age- or stage-structured populations, cannot readily incorporate the formation of disperser groups and new packs. We thus developed an individual-based model of wild dog population and pack dynamics, which is designed to support wild dog conservation management. The model includes social structure and behaviour, but nevertheless is conceptually simple. It is parameterized with data from our 25-year field study (Somers et al., 2008). To meet the criticism often voiced of individual-based models being too complex, a pattern-oriented modelling approach was employed (Grimm et al., 1996, 2005b; Wiegand et al., 2003). Pattern-oriented modelling is a strategy for optimizing model complexity focusing on patterns (i.e. any non-random display of order) as indicators of essential underlying processes and structures in a real system. In our study, such patterns include pack structure and dynamics (see below).

We used our model to evaluate the relative benefits of employing various management strategies for the re-introduction of wild dogs under varying scenarios. The model was designed to predict: (i) a critical initial composition of a re-introduced population (i.e. number of packs and individuals per pack) that maximizes establishment probability and (ii) a logistically feasible intervention regime that ensures persistence of a re-introduced population by intermittently adding packs, which at the same time allows for harvesting disperser groups to be translocated to other re-introduction sites. Apart from the application presented here, exploring the complex interactions between social behaviour and population viability is likely to be important for the conservation management of group living species in general.

2. Methods

2.1. Study area and data collection

Data underlying the model presented here were collected in the c. 900 km^2 Hluhluwe-iMfolozi Park (HiP), which is located in KwaZulu–Natal Province, South Africa. The park, with its subtropical climate, has a diverse topography and the predominant vegetation is bushveld savannah. HiP is enclosed by an electrified fence; however, wild dogs are notoriously difficult to contain within the perimeter fence.

Twenty-two wild dogs were re-introduced into HiP in 1980/1981 after an absence of half a century (Maddock, 1995, 1999; also see Andreka et al., 1999; Krüger et al., 1999). These animals formed a single pack that has persisted up to the present, but to augment decreasing numbers and stimulate breeding activities, a second pack (four animals) was translocated to the park in 1997 (Somers and Maddock, 1999). This was the first implementation of the meta-population management plan for the conservation of wild dogs in South Africa (Mills et al., 1998; also see Moehrenschlager and Somers, 2004; Davies-Mostert et al., 2009), in which the previously largely isolated HiP became linked to other conservation areas through translocations. Another two packs (ten animals in total) were subsequently added to the park in 2001 and 2003 (Graf et al., 2006; Gusset et al., 2006a). At the end of 2004, there were 48 known wild dogs living in six packs (Gusset et al., 2006b).

Data collection is described in detail by Somers et al. (2008). In short, data on the demography of wild dogs were collected from 1980 to 2004 by non-invasive procedures (photographic records and sightings by HiP staff) and from direct observations using radio telemetry. Demographic data were analyzed combining static and cohort life tables, providing data for 41 pack-years. All input values for our model were drawn from this dataset or were calibrated to match an observed pattern (see below) in the population modelled here (Grimm et al., 1996, 2005b; Wiegand et al., 2003).

2.2. The model

The model description follows the standard ODD protocol (i.e. Overview, Design concepts and Details) for describing individual- and agent-based models (Grimm et al., 2006). The model was implemented in C++ using Borland C++ Builder Professional 6.0 (2002). The executable program is provided in the electronic supplementary material and the source code is available from the authors upon request.

2.2.1. Purpose

The model was designed to predict the probability of small reintroduced populations of wild dogs establishing themselves and persisting in the release area under various scenarios, including regular translocation of disperser groups.

2.2.2. State variables and scales

The three entities included in the model were individuals, packs and disperser groups. Individuals were characterized by their state variables sex, age, social status and pack or disperser group membership. A pack was defined as a reproductive unit (either newly formed or established, see below) that contained a dominant pair, potentially also including pups as well as subordinate yearlings and adults of both sexes. Pups were less than one, yearlings between one and two, and adults more than 2 years of age. A disperser group consisted of one or more same-sexed individuals originating from the same pack. Time proceeded in discrete steps of 1 year. The model was not spatially explicit to make it more generally applicable and because disperser groups are highly mobile; however, space was indirectly included in the model by considering the ecological capacity for wild dogs in HiP (see below).

2.2.3. Process overview and scheduling

The fate of each individual in the population was traced from birth to death. Within each year, the following processes were simulated in the given (biologically meaningful and computationally practical) order for each of the given entities: ageing (individuals), reproduction (packs), dispersal (individuals), pack formation (disperser groups), mortality (individuals), catastrophes (individuals), management interventions (packs and disperser groups) and dominance (packs). Individuals, packs and disperser groups were processed in a randomized sequence every year. The rules defining the above processes are described in Section 2.2.7 below.

2.2.4. Design concepts

2.2.4.1. Emergence. Wild dog population and pack dynamics emerged from the behaviour of individuals, but individual behaviour was entirely imposed by probabilistic empirical rules. No Allee effects at the pack level were imposed onto the model, as no such effects were observed in the population modelled here (Somers et al., 2008). However, possible Allee effects were allowed to emerge from the model.

2.2.4.2. Interaction. Four types of interaction were modelled implicitly: (i) within each pack, dispersing individuals of the same sex formed a disperser group, (ii) formation of a new pack was dependent on the encounter of opposite sex disperser groups originating from different packs, (iii) younger yearling or adult males could displace the dominant male, and (iv) dominants of both sexes suppressed subordinate pack members from reproduction.

2.2.4.3. Stochasticity. All demographic and behavioural parameters in the model were interpreted as probabilities using a Bernoulli trial to include demographic stochasticity, and were drawn from empirical probability distributions to include environmental stochasticity. Extreme fluctuations in environmental conditions were represented by random catastrophic events.

2.2.4.4. Collectives. Individuals were grouped into packs and disperser groups that represented independent entities, with some processes being explicitly related to these collectives (e.g. reproduction or formation of new packs).

2.2.4.5. Observation. For model testing, we observed individual life histories process by process (Grimm, 2002), especially regarding pack formation events (Fig. 1). To validate the model, we tested whether five characteristic patterns in population and pack dynamics produced by the model at different hierarchical levels of the system (see below) corresponded to the observed patterns in our study population, including patterns not explicitly considered in model construction. For model analysis, only population-level variables were recorded, most importantly time to extinction, from 1000 model runs that lasted for 1000 years or until the population became extinct. From the distribution of extinction times, we calculated the intrinsic mean time to extinction T_m (in years) using the plot described in Grimm and Wissel (2004). T_m is particularly well suited for characterizing the long-term persistence of small populations (e.g. Melbourne and Hastings, 2008).

2.2.5. Initialization

Simulations started with a specified number of packs and individuals per pack, but no disperser groups. One male and female per pack were randomly selected as dominants. Sex and age of individuals in initial packs was random: the probability of being male was 0.50 and age was uniformly distributed from 1 to 6 years.

2.2.6. Input

The model did not include any environmental variables as driving the population, as competitor density, amount of rainfall and prey availability did not significantly influence the population modelled here (Somers et al., 2008). Environmental variation was represented by environmental stochasticity and random catastrophic events.

2.2.7. Submodels

2.2.7.1. Ageing. The age of all individuals increased by 1 year. All individuals that reached their observed maximum age of 9 years died (Somers et al., 2008).

2.2.7.2. Reproduction. Both males and females could theoretically become dominant and reproduce from 1 to 8 years of age, with only packs that contained a dominant pair potentially reproducing (Somers et al., 2008). The probability of a pack reproducing in a given year was piecewise density-dependent, which best matched the observed linear negative density dependence in population growth rate (Somers et al., 2008). HiP's ecological capacity for wild dogs, based on the availability of the most important prey species, was estimated to be at $N = 62$ (Lindsey et al., 2004), with N being the total number of all adults and yearlings plus half the number of pups. If N was smaller than half of the ecological capacity, a litter was added annually with an observed probability 0.33 to newly formed packs (i.e. in the first breeding season after formation) and with an observed probability 0.66 to established packs (i.e. in all subsequent breeding seasons). Litter size was randomly selected from a binomial distribution whose observed mean value was 7.9 ± 3.5 (SD). Each pup was randomly allocated a sex, where the observed probability of being male was 0.55 (Somers et al., 2008). If N was equal to or larger than half of the ecological capacity, the probability of producing a litter decreased linearly with N until it reached zero at the ecological capacity.

2.2.7.3. Dispersal. Each subordinate young adult (2–4 years of age) considered leaving its natal pack with a calibrated sex-specific annual probability, for males 0.80 and for females 0.90, matching the observed proportion of animals dispersing (Somers et al., 2008). Within each pack, same-sexed individuals willing to disperse formed a disperser group. If such a "group" consisted of one disperser only, this animal actually left with a calibrated probability 0.50; larger sized disperser groups containing two or more individuals invariably left the pack, matching observed disperser group sizes (Somers et al., 2008). Each dispersing individual died during

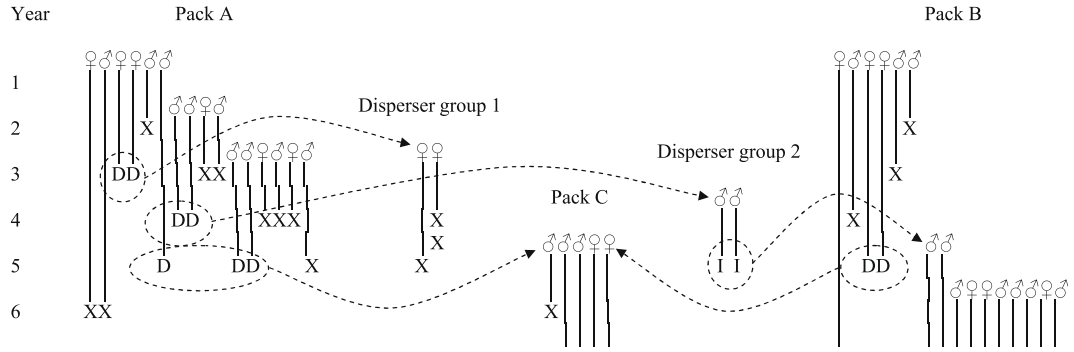

Fig. 1. Example of low-level model testing: predicted 6-year dynamics of a re-introduced wild dog population starting with two packs and six individuals per pack, which matches the observed dynamics in the field (X = death; D = dispersal; I = immigration).

dispersal and prior to pack formation with an observed sex-specific probability, for males 0.45 and for females 0.43.

2.2.7.4. Pack formation. All disperser groups were annually checked once against each other for potential pack formation. If two disperser groups of the opposite sex that originated from a different pack met, the two formed a new pack with probability 0.64, matching observed failures in pack formation (Somers et al., 2008). One male and female were randomly selected as dominants in these newly formed packs. Dispersers that neither died nor formed a new pack remained in the population as non-breeding floaters, with an annual sex- and age-specific probability of dying (see following).

2.2.7.5. Mortality. During each year of the simulation, each individual had an observed sex- and age-specific probability of dying (Somers et al., 2008), for males age 0 = 0.07, age 1 = 0.29, age 2–4 = 0.17, age 5–8 = 0.30 and for females age 0 = 0.16, age 1 = 0.20, age 2–4 = 0.01, age 5–8 = 0.22. If all adults and yearlings in a pack died, any pups left behind also died. In case a dominant died, a randomly selected yearling or adult of the respective sex became the new dominant. The case of no yearling or adult being present in the pack, leaving the dominant position unoccupied, is described below.

2.2.7.6. Catastrophes. A catastrophe (e.g. a disease outbreak) occurred with an annual probability 0.04, matching the observed catastrophe frequency (Somers et al., 2008). Due to the relatively small size of conservation areas used for wild dog re-introductions, such a catastrophe was assumed to affect the whole population. If a catastrophe occurred, each individual died with probability 0.42, matching the observed catastrophe severity (Somers et al., 2008).

2.2.7.7. Management interventions. Management interventions were characterized by two time intervals, *IntroducePack* and *HarvestGroup* (in years). These two parameters reflect management decisions to translocate wild dogs from or to a conservation area: real removals usually happen by capturing whole disperser groups and additions by releasing entire packs, as packs for release are typically formed in pre-release holding facilities by artificially bonding opposite sex disperser groups of different origin (Gusset et al., 2006a). After every *IntroducePack* interval, a newly formed pack was added to the population, with a uniformly distributed size of between four and eight animals, including a dominant pair, and random sex and age (see "Initialization" above). After every *HarvestGroup* interval, a randomly selected disperser group, if available, was removed ("harvested") from the population.

2.2.7.8. Dominance. In each pack, the dominant male was displaced by a randomly selected younger yearling or adult male with an observed probability 0.20 (Somers et al., 2008). The displaced male then remained in the pack as a subordinate. If one dominant position remained unoccupied after a dominant died (see above), a randomly selected disperser group of the respective sex joined the pack and one randomly selected immigrant male or female became the new dominant. If no disperser group of the respective sex was present or if both dominants died, the pack split into single sex disperser groups.

3. Results

3.1. Model testing

The model was validated by comparing five characteristic output variables (or patterns, sensu Wiegand et al., 2003) of the model to their corresponding values observed in the field (Somers et al., 2008). A re-introduced wild dog population, which mimicked the dynamics of our study population (see above), was simulated 1000 times over 25 years. The predicted values from the model compared favourably to the observed values from our 25-year field study, including the values' variation (Table 1). This suggests that the model is valid enough for its intended purpose, as it could reproduce multiple output patterns observed at different hierarchical levels of the system, which were not imposed onto the model but emerged from interactions between the simulated individuals, packs and disperser groups. Particularly the proportion of vacant dominant positions that were filled by floaters and the proportion of disperser groups that failed to form a new pack are strictly emerging properties of the model (Table 1). The robustness of the model was evaluated by conventional sensitivity analysis of all model parameters (Possingham et al., 2001), where each param-

Table 1
Comparison of model predictions and field observations for five aggregated state variables characterizing a re-introduced wild dog population. Predicted values were not calibrated or imposed onto the model but emerged from interactions between the simulated individuals, packs and disperser groups.

	Parameter value (mean ± SE)	
	Predicted	Observed[a]
Annual pack size	8.3 ± 1.1	8.1 ± 1.1
Annual population sex ratio (proportion males)	0.53 ± 0.03	0.56 ± 0.03
Annual population age ratio (proportion pups)	0.23 ± 0.04	0.26 ± 0.05
Proportion of vacant dominant positions filled by floaters	0.56	0.50
Proportion of disperser groups failed to form new pack	0.41	0.43

[a] Parameter values from Somers et al. (2008).

eter was varied separately by ±10% of its mean value (rounded to integer if required). The analysis showed a moderate sensitivity *s* of the individual parameters (*s* = ratio of the relative change in T_m to the relative change in parameter value) (Table 2).

3.2. Model application

Simulations showed that a small re-introduced population of wild dogs has a considerably lower chance of long-term persistence without intermittent supplementation, largely independent of initial conditions (Fig. 2). Note that an intrinsic mean time to extinction T_m of 10,000 years corresponds to an extinction risk of 1% in 100 years (Grimm and Wissel, 2004).

In Fig. 3, to quantify a critical initial composition for a re-introduced wild dog population to establish itself in the release area, initial number of packs and individuals per pack were varied over a range of 1–4 packs (four rows of panels) and 2–8 individuals per pack (four columns of panels). Simultaneously, to determine an intervention regime that ensures persistence of the re-introduced population, the interval of adding packs (*x*-axis of each panel) and harvesting disperser groups (*y*-axis of each panel) was varied over a logistically realistic range from 2 to 10 years. The figure shows contour plots interpolated in Systat SigmaPlot 10.0 (2006).

When simply looking at initial composition (outer axes of panels in Fig. 3), the chance of establishment levelled off after a minimum initial release of two packs and six individuals per pack. When incorporating management interventions (inner axes of panels in Fig. 3), the chance of persistence was highest when packs were added at least every 6 years, which allowed for harvesting disperser groups as often as every 4 years. Long-term persistence is virtually impossible if a population starts with a single pack (lowest row of panels in Fig. 3), unless it is frequently supplemented (leftmost data in all panels in Fig. 3; also see Fig. 2). Given sufficient prey, the interval of adding a pack (*x*-axis of each panel in Fig. 3) seems to be the most important factor governing the persistence of a small re-introduced wild dog population.

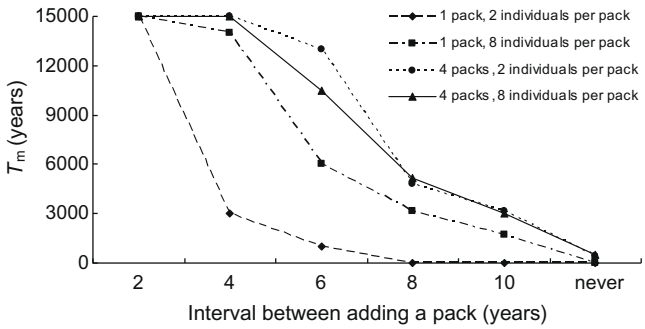

Fig. 2. A small re-introduced wild dog population has a short intrinsic mean time to extinction T_m without intermittent supplementation (i.e. "never" on *x*-axis; initial conditions: one or four packs and two or eight individuals per pack; supplementation: packs uniformly distributed in size from four to eight individuals; no removals).

The undulating pattern in T_m for some parameter combinations in Fig. 3 was triggered by simultaneous supplementation and removal events (e.g. a 6-year interval of both adding a pack and harvesting a disperser group). This indicates that the relative timing of supplementation and removal events is important: disperser groups preferably should not be harvested in the same year as a pack is added to the population, even if this entails a shorter harvesting interval. The reason for this is that adding a pack unfolds its positive effect on population persistence mainly if no disperser group is harvested in the same or the following year. For any predetermined initial composition, Fig. 3 allows for assessing the extent of supplementation necessary to ensure population persistence, which then allows for evaluating how often a disperser group can be harvested from the small source population.

Table 2
Model parameters, reference values and results of the local sensitivity analysis for a re-introduced wild dog population (initial condition: two packs and six individuals per pack; intervention regime: supplementation every 6 years and removal every 4 years).

Parameter[a]	Reference value[b]	Sensitivity[c]	
		+10% of parameter value	−10% of parameter value
Reproduction in newly formed packs (*p*)	0.33	1.13	−0.93
Reproduction in established packs (*p*)	0.66	10.10	−5.18
Litter size (*v*)	7.9 ± 0.8	4.06	−3.32
Primary sex ratio (*p*)	0.55 ± 0.06	−1.19	0.02
Ecological capacity (*v*)	62	0.49	−0.44
Density dependence threshold (*v*)	31*	1.67	−2.41
Dispersal in males (*p*)	0.80*	−0.06	1.10
Dispersal in females (*p*)	0.90*	−1.10	1.84
Disperser group size threshold (*v*)	2*	0.37	−0.66
Pack formation (*p*)	0.64	−0.45	−0.37
Dominant displacement (*p*)	0.20	1.28	−0.33
Mortality in male pups (*p*)	0.07 ± 0.06	−0.08	0.36
Mortality in female pups (*p*)	0.16 ± 0.14	−1.00	−0.98
Mortality in yearling males (*p*)	0.29 ± 0.14	−0.13	0.65
Mortality in yearling females (*p*)	0.20 ± 0.20	−0.96	2.12
Mortality in young adult males (*p*)	0.17 ± 0.08	0.46	0.68
Mortality in young adult females (*p*)	0.01 ± 0.01	−0.32	−0.72
Mortality in old adult males (*p*)	0.30 ± 0.16	−1.79	2.93
Mortality in old adult females (*p*)	0.22 ± 0.16	−2.92	4.69
Dispersal mortality in males (*p*)	0.45	−1.57	1.19
Dispersal mortality in females (*p*)	0.43	−2.25	1.20
Longevity (*v*)	9	2.71	−2.34
Catastrophe occurrence (*p*)	0.04	−1.89	1.47
Catastrophe severity (*p*)	0.42	−2.86	5.00

[a] *p* = probability, *v* = absolute value.
[b] Reference values from Somers et al. (2008) or calibrated to match an observed pattern in the population modelled here (indicated by an asterisk). Measures of precision could not be assigned to values that represent proportions.
[c] Sensitivity = ratio of the relative change in T_m to the relative change in parameter value.

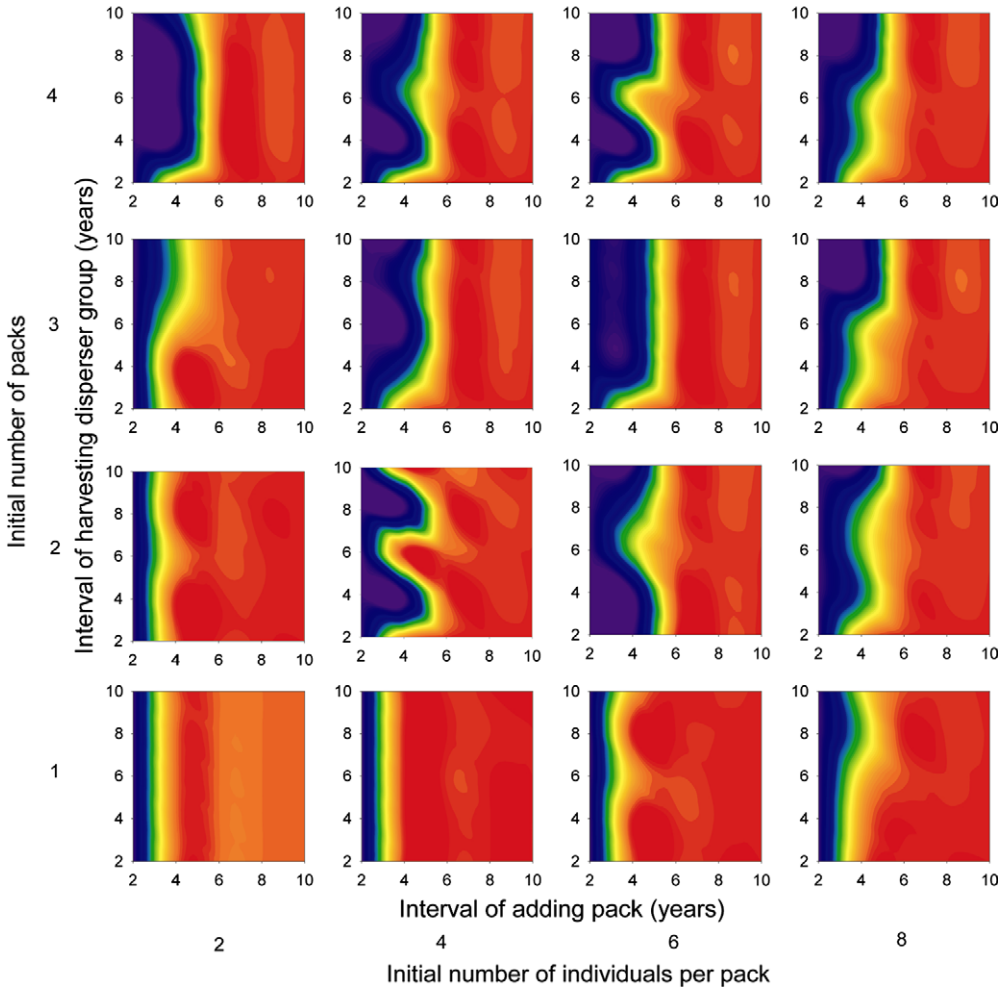

Fig. 3. Interpolated contour plots of the intrinsic mean time to extinction T_m (red–orange: T_m < 10,000 years, yellow–green–blue: T_m > 10,000 years) of a small re-introduced wild dog population under different initial conditions (outer axes of panels: 1–4 packs and 2–8 individuals per pack) and intervention regimes (inner axes of panels: supplementation and removal every 2–10 years). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Our model appears to capture the essential characteristics of a real wild dog population, while being conceptually simple. The five output variables that we looked at to validate our model are of course not independent of the input parameters, which included some calibration. However, although these output variables were not explicitly considered during model development and calibration, they matched the observed values (Table 1). Our validation procedure thus ensured that the model correctly captures internal relationships between variables and to some degree the internal organisation of the real system (Rykiel, 1996). Individual-based models have been criticized for being too "data hungry" (Morris and Doak, 2002), but using a pattern-oriented approach can considerably decrease the amount of data needed. A model can be evaluated by how well it can reproduce multiple patterns observed at different hierarchical levels of the system, even in the absence of long-term census and demographic data (Grimm et al., 1996, 2005b; Wiegand et al., 2003). Our model appears to be relatively robust to parameter uncertainty (Table 2), collectively suggesting that it is structurally realistic (Wiegand et al., 2003) enough to place confidence in inferences about real wild dog populations based on modelling results.

Compared to other population viability analyses of wild dogs (Burrows et al., 1994; Ginsberg et al., 1995; Ginsberg and Woodroffe, 1997; Mills et al., 1998; Vucetich and Creel, 1999; Cross and Beissinger, 2001; Creel and Creel, 2002; Creel et al., 2004; Vial et al., 2006), which highlight the role of interspecific competition, ecological capacity, disease outbreaks and age-specific mortality, our sensitivity analysis revealed that an additional important factor may be dispersal mortality (Table 2). Similar to the canid model of Pitt et al. (2003), our model also suggests that floating disperser groups buffer a population's reproductive capacity from a loss of breeding individuals. In the HiP wild dog population, the proportion of vacant dominant positions that were filled by floaters was 56% (predicted) and 50% (observed), respectively (Table 1). Our findings were confirmed for other wild dog populations (Creel and Creel, 2002) and by Courchamp et al. (1999) for cooperative breeders in general. To link the currently isolated conservation areas containing wild dogs through natural dispersal, increased tolerance of dispersing wild dogs will be necessary (Gusset et al., 2008a,b), thereby reducing the need for costly translocations. Similar considerations regarding dispersal mortality seem to apply for the persistence of disjunct populations of other group living species in human-dominated landscapes (e.g. Haight et al., 1998).

The sensitivity of our model to dispersal mortality provides a direct link to the simulated pack formation process, which can be limited by a lack of dispersers. In contrast to previous wild dog models (Vucetich and Creel, 1999; Courchamp et al., 2000, 2002; Boukal and Berec, 2003; Vial et al., 2006), we did not impose an Allee effect at the pack level directly onto our model, as no such effects were observed in the population modelled here (Somers

et al., 2008). Instead, a mate-finding Allee effect – which arises when potentially reproductive dispersers of each sex fail to meet and thus forego reproduction – emerged from individual behaviour when trying to form new reproductive units at low pack numbers. In the HiP wild dog population, the proportion of disperser groups that failed to form a new pack was 41% (predicted) and 43% (observed), respectively (Table 1). Mate shortage, which may be intricately linked to aspects of mate choice also incorporated into our model (Berec and Boukal, 2004), has been shown to limit establishment success and prevent range expansion in species subject to Allee effects (Keitt et al., 2001). Our study therefore emphasizes the potential importance of mate-finding Allee effects for population persistence probably in a variety of group living species (e.g. Schenck et al., 2002; Hurford et al., 2006).

Based on these considerations limiting pack formations, our model enabled us to quantify a critical initial number of packs and individuals per pack (cf. Courchamp et al., 2002; Rasmussen et al., 2008) necessary for a re-introduced wild dog population to establish itself in the release area (Fig. 3). The model also allowed us to determine a logistically realistic intervention regime at which a re-introduced wild dog population had the best chance of persistence, intermittently adding packs and harvesting disperser groups for translocation to other release sites, without threatening the small source population (Fig. 3). If levels of natural dispersal are not sufficient to ensure meta-population viability (Fig. 2), our findings indicate that re-introduction programmes may require continuous translocations, as currently applied to wild dogs in South Africa (Gusset et al., 2008a; Davies-Mostert et al., 2009). This need for regular translocations may also reflect the transient nature of the species (Creel and Creel, 2002), a largely neglected but possibly important aspect for the conservation of other small wild dog populations. Models, as the one presented here, are indispensible for assessing sustainable harvesting rates in such small populations, as including data on social structure and behaviour improves estimates of population viability (Gerber, 2006). Our individual-based model, therefore, could serve as a starting point for future planned re-introductions of group living species in evaluating practically feasible release and intervention protocols under varying conditions, making costly re-introduction attempts as efficient as possible. It will be relatively easy to parameterize the model for other populations, make it spatially explicit and manipulate other parameters.

In conclusion, our thorough quantitative analysis of possible conservation outcomes provides insight into how populations made up of social groups have dynamics, and ultimately persistence, determined by individual behaviour, promoting individual-based ecology (Grimm and Railsback, 2005) as a unifying approach to link traits on the individual level to system-level properties.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.07.007.

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